SEXUAL AND AGGRESSIVE BEHAVIORS

IN TWO INBRED STRAINS OF MICE

By

DIRK WALTER MOSIG

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL OF THE
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DEDICATION

To Edna,

with love...

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IN TWO INBRED STRAINS OF MICE

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Data regarding the copulatory behavior of widely used
research animals--inbred strains of house mice, Mus mus-
culus--are presented. In order to assess inter-laboratory
variability, nine males of the AKR/J strain each received
three tests of copulatory behavior. With some exceptions,
results indicate a general similarity across laboratories.
In order to provide the first quantitative description of
copulation in the widely used C3H/HeJ strain, nine males
received similar treatment. While basic motor patterns
were identical to other strains, C3H/HeJ are the slowest
copulating animals of any strain yet reported.

One or two ejaculations were attained in all tests.
Quantification of copulatory behavior preceding the second

ejaculation revealed a general facilitation of behavior
relative to the behavior preceding the first ejaculation.
A change of female following the first ejaculation produced
a further facilitation of later behavior--particularly in
AKR/J mice. Results are related to theories of the control
of sexual behavior.

In order to search for a relationship between sex and
aggression, measures of copulatory behavior were correlated
with five measures of aggressive behavior. Although AKR/J
males were both more aggressive and faster copulators than
C3H/HeJ males, no correlation was found among individual
differences in measures of aggressive and copulatory be-
haviors.

INTRODUCTION

The present research was conducted in order to provide new data regarding the copulatory behavior, and the relationship between copulatory behavior and aggressive behavior, in inbred strains of house mice Mus musculus.

The house mouse is the most widely used laboratory mammal. Well over one million mice are raised each year in the U. S. alone for biomedical (e.g., bacteriology, cancer, genetics) and behavioral research (Snell, 1941).

House mice can be bred, housed, and maintained easily. A large number of inbred strains of Mus musculus is available from commercial suppliers. Inbred animals, the outcome of mating close relatives for many generations, provide a means to control the genotype, and determine the effect of genetic variables on observable behavioral patterns, such as copulation.

Copulatory behavior is an important part of the behavioral repertoire of any species. As an essential component of reproductive behavior, it is significantly involved in the survival of the species. Patterns of copulatory behavior vary widely among different mammalian species, although they tend to be quite stereotyped for individuals within a given species. The between-species

variability as well as the within-species stereotypy is probably the result of the action of strong selective pressures for successful reproduction (Dewsbury, 1972).

Complete descriptions of the copulatory behavior of any species should include careful and detailed quantitative and qualitative analyses of the motor patterns involved. Standardized measures and testing procedures should be used. Such descriptions should also include data on courtship, satiety, and recovery of sex drive. In addition, complete descriptions of sexual behavior ought also cover a great variety of genotypes, particularly those used in other types of research.

House mice are ideal experimental animals for the study of copulation, due to their easily observable and stereotyped behavior. Standardized measures and testing procedures are available, and allow for the ready quantification of the different aspects of the mating behavior of Mus musculus.

Sexual Behavior

The copulatory behavior of several strains of the house mouse Mus musculus has been described (Keeler, 1931; Lewis and Wright, 1935; King, 1956; Lipkow, 1960; van Oortmerssen, 1970) and quantitatively analyzed (McGill, 1962, 1969; McGill and Blight, 1963; Levine, Barsel, and

Diakow, 1966; McGill and Ransom, 1968; Vale, Lee, and Ray, 1970; Vale and Ray, 1972).

The copulatory behavior of the male mouse consists essentially of a "series" of mounts and intromissions, resulting in ejaculation. This is followed by a post-ejaculatory interval (PEI), or refractory period, which precedes the resumption of copulatory behavior. A more detailed description of the general motor patterns involved can be found in the Results section below.

A careful examination of the various descriptive and quantitative studies listed above reveals that they fall short of a complete description of copulatory behavior.

In the first place, there is a lack of cross-labora-tory validations. Most of the strains studied have been reported by a single investigator, and most results ob-tained have not been replicated. In the few instances that the same strain has been described by different observers, in different laboratories, there has been less than perfect agreement (e.g., McGill, 1962, and Vale, Lee, and Ray, 1970; McGill and Blight, 1963, and Vale and Ray, 1972).

Inter-laboratory variability can be affected by un-controlled or unreported extraneous factors. For instance, the part of the diurnal cycle during which animals are tested must be taken into consideration, when comparisons between data reported in different studies are to be made. Measures of copulatory behavior in rats are significantly affected by the hour of testing within the dark phase of

the diurnal cycle (Dewsbury, 1968). Mice show activity peaks at dusk and just before dawn (van Oortmerssen, 1970).

The age at which animals were tested differs between studies, and may account for some discrepancies. Another important factor is the illumination level used in the testing situation, which may affect the behavior of the animals (Klein, Howard, and De Fries, 1970). Unfortunately, many studies fail to report the light levels under which testing is conducted, as well as other possibly relevant variables.

One purpose of the present research is to attempt to replicate and extend the observations by McGill and Ransom (1968) of the copulatory behavior of AKR/J male mice. This will help to determine the extent of inter-laboratory variability. Laboratory and experimenter effects are variables that must be taken into account if meaningful comparisons are to be made between the results obtained by different investigators.

In the second place, a complete description of the copulatory behavior of the house mouse should cover many genotypes, but only a few have been studied. The present study adds a new strain, C3H/HeJ, whose copulatory behavior has not been described, although C3H mice have been used in various investigations (e.g., Southwick and Clark, 1966; Vale, Vale, and Harley, 1971).

Thirdly, all of the above data are limited to the

behavior during the first ejaculatory series. This paucity
of satiety data is surprising, when compared with the abun-
dant information on satiety and recovery of sex drive in
other species, such as the rat Rattus norvegicus (e.g.,
Beach and Jordan, 1956; Larsson, 1956). This is perhaps
due in part to the generally longer time period needed to
achieve multiple ejaculations in the mouse. No mouse has
ever been reported to have achieved more than two ejacula-
tions within a 24-hour period (McGill, 1965), while it is
not uncommon for a male rat to achieve seven successive
ejaculations within a few hours (Beach and Jordan, 1956).

Several theoretical models of sexual behavior have
been proposed (e.g., Young, 1961; McGill, 1965). These
theories include several hypothetical mechanisms involved
in sexual arousal, satiety, and recovery. At least one
of these theories is based on observations of the copula-
tory behavior of Mus musculus (McGill, 1965). The lack
of satiety data for the house mouse means that some major
implications of these theoretical models have not been
tested.

Since several hypotheses in the present research are
derived from theoretical models of sexual behavior, these
models will be briefly considered here.

The dual mechanism theory (Beach, 1956; Beach and
Jordan, 1956) basically holds that sexual behavior in male
rats is initiated by a sexual arousal mechanism (AM). As
the level of arousal is increased, the copulatory threshold

is crossed, and the male mounts the female. The first intromission activates a second mechanism, the copulatory mechanism (CM). The level of excitement increases with each successive intromission, until the ejaculatory threshold is crossed and ejaculation occurs. Because the second ejaculatory series is completed in less time and with fewer mounts and intromissions (less stimulation) than the first one, Beach postulated that the CM is sensitized by the first series. Beach and Whalen (1959) obtained data indicating that both the AM and the CM are sensitized by a copulatory series, so that neither the AM nor the CM are depressed by the ejaculation. Satiety and the recovery of sex drive following the ejaculation, measured by the post-ejaculatory interval (PEI), were attributed to non-sexual fatigue effects.

McGill (1965) found the dual mechanism theory inadequate to account for data obtained on the copulatory behavior of mice, and suggested a modification to the theory, adding a third mechanism to account for the PEI. This was the ejaculatory mechanism (EM), which is discharged by the ejaculatory reflex. McGill found that, contrary to predictions of the dual mechanism theory, measures obtained from the copulatory behavior of male mice showed no correspondence between mount latency (ML) and PEI, and thus proposed that the ML and the PEI do not measure the same mechanism. The triple-mechanism theory includes the AM, measured by the ML and sensitized by intromissions and

ejaculations; the CM, measured the ejaculation latency (EL) and also sensitized by intromissions and ejaculations; and the EM, which is discharged by the ejaculation and measured by the PEI. The EM prevents sexual arousal until some recovery has occurred. It is progressively depressed, if full recovery is not allowed to take place between ejaculations. Consequently, the time necessary for recovery increases.

If the CM is sensitized by intromissions and ejaculations, and measured by the EL, the latency for the second ejaculation (EL-2) should be shorter than the first ejaculation latency (EL-1). This prediction has not been tested in house mice because previous studies have not included data collected during the second ejaculatory series (i.e., between the first and second consecutive ejaculations). The present study is intended to fill this gap in the current understanding of the copulatory behavior of the house mouse, by providing such data.

Assuming that the EM is discharged by the ejaculation, and that successive ejaculations result in a progressively greater depression of the EM, are there any variables which affect the recovery of the EM? The introduction of a fresh female replacing the original one, either between ejaculatory series or after a satiety criterion has been reached, appears to be one such factor.

When a fresh female partner is substituted for the original one, after the animal has reached an exhaustion

or satiety criterion, an apparent recovery of sex drive
occurs, and the male often achieves one or more additional
ejaculations. This phenomenon, extensively studied in the
rat, is known as the "Coolidge effect" (e.g., Fowler and
Whalen, 1961; Fisher, 1962; Wilson, Kuehn, and Beach, 1963;
Beach and Ransom, 1967; Bermant, Lott, and Anderson, 1968).
Nevertheless, the above studies report only a small number
of additional ejaculations, compared to the performance of
the sexually rested male.

Although Hsiao (1965, 1969) did not find a similar
effect when he attempted to replicate Fisher's (1962) ex-
periment, the "Coolidge effect" data support the view that
the sexual "exhaustion" of the male rat is not simply the
product of cummulative non-sexual fatigue effects, but
rather the combined outcome of several variables, including
habituation or lowered responsiveness to a constant sexual
stimulus, and a general reduction in sexual excitability
(Beach and Ransom, 1967).

A different phenomenon is the effect on the recovery
of sex drive of introducing a fresh female between copu-
latory series, rather than after an exhaustion criterion
has been reached. The data of Clemens (1969) on the deer-
mouse Peromyscus maniculatus gambeli appear to indicate
that this may be an important manipulation. Nevertheless,
no effect of this variable on the recovery of sex drive
was found in other species, such as the rat Rattus norvegi-
cus (Hsiao, 1965; Dewsbury, 1968; Tiefer, 1969). The ef-

fect of a change of female after each ejaculation of the
male has not been reported for the mouse Mus musculus. The
lack of these data, as well as the lack of data on the
"Coolidge effect" in house mice, is a fourth major gap in
the present knowledge of the copulatory behavior of Mus
musculus. To partially remedy this situation, the present
study presents data showing the effect of substitution of
a female, immediately following the first ejaculation, on
the copulatory behavior and recovery of sex drive of AKR/J
and C3H/HeJ male mice.

Interaction Between Sex and Aggression

Copulatory behavior is usually well defined and can be
considered as a sequence of events initiated by a hypothet-
ical arousal mechanism and ending in ejaculation. Aggres-
sive behavior cannot be explained in terms of a similar
model, however, because the label "aggressive" has been
applied to many diverse and basically unrelated behavioral
patterns. Several different types of aggression have been
proposed, each with a different physiological basis and
different behavioral goals (Moyer, 1968a). All measures
of aggression reported in the present research are meas-
ures of inter-male aggression, which is released by the
presence of a male conspecific to which the attacker has
not become habituated (Moyer, 1968b).

The various behavioral patterns and postures involved in the aggressive behavior of _Mus_ _musculus_ have been described (e.g., Scott and Fredericson, 1951; Calhoun, 1956; Grant and Mackintosh, 1963; Clark and Schein, 1966; Scott, 1966; Calhoun, 1968). They include exploring, orienting, approaching, sniffing, pushing, sparring, wrestling, tail-thumping, biting, freezing, squealing, chasing, jumping, escaping, moving away, and self-grooming, and a variety of stereotyped postures.

Differences in the aggressive behavior of 14 strains have been demonstrated by Southwick and Clark (1966). Several cross-fostering experiments have been performed to determine the relative importance of heredity and environment in the aggressive behavior of the laboratory mouse (Fredericson, 1952; Fredericson and Birnbaum, 1954; King, 1957; Southwick, 1968).

There are several reasons why a correlation between sexual and aggressive behaviors may be expected:

1. Both sex and aggression are affected by hormones in similar ways (Beeman, 1947; Champlin, Blight, and McGill, 1963; Edwards, 1969; Whalen, 1968).

2. Aggressive animals have often, but not always, been reported to be also more successful copulators (Levine, 1958, 1962; Levine, Diakow, and Barsel, 1965; Levine, Barsel, and Diakow, 1965).

3. The dominance of sex over aggression, or vice versa, appears to be a function of the genotype. C57BL/10

males stopped fighting following the introduction of an estrous female, while under similar circumstances BALB/c,Sc males continued their aggressive interaction (Fredericson, Story, Gurney, and Butterworth, 1955).

4. Experience with defeat sometimes results in sexual avoidance (Kahn, 1961). Nevertheless, severe defeat was not found to be an effective suppressor of copulatory behavior (Vale and Lee, 1968a) and has little effect upon reproductive vigor (Vale and Lee, 1968b). Dominant males may tend to be more successful sexually, not because they have a stronger sex drive, but because their status affords them free movement and access to any female (King, 1956).

5. Continuous aggression or the threat of it affects the frequency, but not the pattern of copulatory behavior, and is accompanied by a significant increase in adrenal weight. Nevertheless, no relationship has been found between testis and seminal vesicle weights, and inter-male aggression, in several inbred strains of mice (Vale, Vale, and Harley, 1971; Vale, Lee, and Ray, 1970). The above authors hypothesized that aggression may act upon the threshold of sexual behavior through the hypothalamic-pituitary-adrenocortical axis rather than through the reproductive glands.

It is not possible to conclude that a single underlying physiological mechanism controls both copulatory and aggressive behaviors. Instead, it seems likely that there is a complex interaction between the mechanisms controlling

sex and aggression. The present investigation includes an attempt to find a correlation between intra-strain and inter-strain fighting success, on the one hand, and copulatory behavior on the other.

The Present Research

In summary, the present study was designed to supply data to fill several important gaps in the current knowledge of the copulatory behavior of <u>Mus musculus</u>. These gaps consist of the absence of cross-laboratory validations; the small number of strains that have been studied; the lack of information on second series behavior, with or without a change of female partner, and the lack of data on a possible correlation between measures of copulatory and aggressive behaviors.

The objectives of the present study are:

1. To record the copulatory behavior of AKR/J males during the first copulatory series, and to compare the results with those obtained by McGill and Ransom (1968) in order to examine inter-laboratory variability.

2. To describe for the first time the copulatory behavior of C3H/HeJ males.

3. To describe the behavior of both AKR/J and C3H/HeJ males during the second copulatory series, and test implications of theoretical models of sexual behavior in <u>Mus musculus</u>.

4. To determine the effect of a change of female between copulatory series.

5. To search for a correlation between quantitative measures of aggressive behavior and measures of copulatory behavior.

METHOD

Subjects

The inbred mice used in the present study were of the strains AKR/J and C3H/HeJ.

A total of 32 males and 50 females of each strain, or a grand total of 64 males and 100 females, were obtained from the Jackson Laboratory, Bar Harbor, Maine. However, because several animals failed to mate, or died before the conclusion of the experiments, a much smaller number of mice completed the tests, as noted in the Results section below.

The animals were received in two shipments. The first group consisted of 12 males and 20 females of each of the two strains. The second shipment included 20 males and 30 females of each of the two strains.

Data on the "Mating Tests" described below were obtained from animals in both shipments. Data on the "Aggression Tests" were obtained from animals in the first shipment, and data on the "Mating Tests with Change of Female" were obtained from mice in the second shipment only.

All animals were approximately six weeks old at the

time of arrival in the laboratory, and were earpunched for identification purposes.

Apparatus

All animals were housed in clear plastic cages. The males' cages were 29 x 19 x 13 cm; the females' were 48 x 27 x 13 cm. The insides were lined with commercially produced litter material.

Tests were conducted in three plexiglass arenas 38 cm in diameter and 60 cm high. The arenas were placed on a wooden table, and filled to one inch with a commercially produced litter material.

Behavioral events were recorded manually on an Ester-line-Angus operations recorder. Light was provided by a 25-watt red light bulb approximately 25 cm from the arenas.

In order to eliminate extraneous sources of sound and light, the arenas were at first surrounded with sheets of heavy black cardboard. This arrangement was used for the "Mating Tests" and "Aggression Tests" described below. Later the arenas were moved to a sound-deadened room, where the "Mating Tests with Change of Female" were conducted.

Attack latencies in tests of aggression were measured with a stopwatch.

Procedure

A. General Maintenance

Males were housed in isolation for four weeks prior to testing and throughout the experiments, while females were housed in groups of five.

All animals had continuous access to water and Purina Lab chow throughout the experiments.

The colony room was maintained on a 12:12 light:dark cycle, with lights going out at 8:00 A.M. and coming on at 8:00 P.M.

B. Mating Tests

All animals were handled and placed in the experimental arena for 10-minute periods, twice a week, during the four weeks prior to testing.

Each animal was tested as soon as possible upon reaching an age of 10 weeks. Males were tested with females of their own genotype. No attempt was made to pair a given male with a particular female in successive tests. Males and females were not tested more frequently than once every two weeks.

All tests were initiated between 8:30 and 10:00 A.M. In each test, the male was allowed 5 minutes in the arena prior to the introduction of the female. Tests were terminated and scored "negative" if intromission did not occur within 15 minutes of the introduction of the female. If

an intromission occurred within that period, tests were
continued until the occurrence of either a second ejacu-
lation or a 90-minute period with no intromissions.

Each male was tested until he achieved either three
"positive" or successful tests, or ten successive "nega-
tive" tests, whichever came first.

Females were brought into behavioral estrus with i.m.
injections of .035 mg of estradiol benzoate, administered
approximately 48 hours before testing, and 0.1 mg of pro-
gesterone 6-8 hours before testing.

All observations in this and the following experiments
were made by the present author.

C. Mating Tests with Change of Female

Six AKR/J males and six C3H/HeJ males that had com-
pleted three positive mating tests were given two addition-
al tests of copulatory behavior. During one of these tests,
the female was removed immediately following the first
ejaculation, and replaced with an unmated female. The test
was then continued until the second ejaculation. During
the other test, the female was removed for a 30-second
period immediately following the first ejaculation, and
then re-introduced in the testing arena. This served as
a control for the effect of removing the female. Three
randomly selected males of each strain received the control
test first, and the other three, the experimental test.

Procedural details were the same as in earlier mating
tests described above.

D. Aggression Tests

Five AKR/J and nine C3H/HeJ males which had completed
mating tests (B) were used. Each male was fought round
robin, first with each other male of his own strain, and
then with every male of the other strain. Both males were
introduced simultaneously to the test arena at the begin-
ning of a bout. A test was terminated with the occurrence
of the first vigorous attack, or at the end of 15 minutes,
if no aggressive behavior had taken place. Subjects were
separated following 5 seconds of vigorous fighting, in
order to avoid serious injury and/or the formation of dom-
inance.

Measures

A. Mating Behavior

The following standard measures of the copulatory
behavior of mice, adapted from McGill (1962), were used:

Mount Latency (ML) - the time in seconds from the
introduction of the female to the first mount with pelvic
thrusting by the male.

Intromission Latency (IL) - the time in seconds from
the introduction of the female until the first thrust with
vaginal intromission by the male.

Ejaculation Latency (EL) - the time in seconds from
the first intromission of a series to the terminal ejacu-
lation of that series.

Total Number of Thrusts (TNT) - the total number of intromission thrusts for all intromissions preceding ejaculation in a given series.

% Bite - percentage of times the male bites the female following the ejaculation duration.

Ejaculation Duration (ED) - the number of seconds the male spends clutching the female and maintaining intromission during, and following, the ejaculation.

Mean Time of Intromission (MTI) - the mean time in seconds from the beginning of a mount with intromission until the male dismounts.

Number of Head Mounts (NHM) - the number of times the male attempts copulation from the front, mounting the head of the female, during a given series.

Mean Inter-Intromission Interval (MIII) - the mean time in seconds from the end of one mount with intromission to the beginning of the next.

Time of Mount (TM) - the duration, in seconds, of a mount without intromission. MTM stands for the Mean Time of Mount.

Mean Pre-Intromission Mount Duration (MPIMD) - the mean time in seconds from the beginning of a mount until the first thrust with intromission within the same mount.

Number of Mounts (NM) - the number of mounts without intromission within a given series.

Number of Intromissions (NI) - the number of mounts with intromission preceding the ejaculation in a given series.

Thrusts per Intromission (T/I) - the number of thrusts with intromission within each mount with intromission.

Post-Ejaculatory Interval (PEl) - the time in seconds from the ejaculation to the resumption of copulation as indicated by the first intromission of the next series.

Pre-Ejaculatory Thrusts (PEI) - the number of thrusts with intromission preceding the ejaculation during the final mount with ejaculation for a given series.

Mating Quotient (MQ) - was computed by taking the ratio of positive to negative copulatory trials for each subject.

B. Aggressive Behavior

The following measures of aggressive behavior were used in the present study:

Mean Attack Latency (MAL) - the mean time in seconds from the introduction of both males to the test arena to the first attack by a given animal. An animal is said to "attack" if it starts wrestling and/or moves to bite its opponent.

First Attack (FA) - the number of times a given male initiated aggressive interaction during a fighting bout.

Number of Wins (NW) - the number of bouts won by a given animal. An animal is scored for a "win" if:

a. the aggressive interaction is terminated by its opponent's escape behavior,

b. at the time the aggressive interaction

is stopped, the animal has held the initiative,
taken a top aggressive posture more frequently,
or bitten its opponent more often.

Tail Rattling (TR) - the number of times an animal is
first to rattle or thump its tail during a bout.

Total Score for Aggression (TSA) - a composite score
calculated by adding first attack, first to tail-rattle,
and number of wins for each animal.

RESULTS

Mating Behavior

A. Basic Motor Patterns

The basic motor patterns of the copulatory behavior
of AKR/J and C3H/HeJ consisted of mounts, intromissions,
thrusts, and ejaculations. A mount was preceded by pursuit
of the female. During the mount, the male held the fe-
male's sides with his forepaws, while performing a series
of rapid, shallow pelvic thrusts. If the male failed to
achieve intromission, as was often the case, he dismounted
as the female moved away, and the interaction was recorded
as a simple "mount." If the male achieved intromission
during the mount, the speed of thrusting was reduced, and
a series of deep thrusts followed. The event was recorded
as an "intromission." The intromission thrusts were dif-
ferentiated from the thrusts without intromission, by their
rate and depth. The male kept one hindfoot on the ground
and the other high on the female's hindquarters. A recep-
tive female characteristically planted her feet on the
ground and assumed the lordotic position, which consisted
of an elevation of her hindquarters and tail, maintaining
this stance until the male dismounted. The ejaculation

terminated a series of intromissions. During the ejaculatory intromission, the speed of thrusting increased markedly, and at the moment of ejaculation, a trembling or shaking was visible in the male, which was now clutching the female with all four limbs, and usually fell to his side, often overturning the female as well. In some cases, the male remained in the mount position, without falling over, throughout the ejaculation. In either case, the ejaculatory position was maintained for as long as 35 seconds. This period was recorded as the "ejaculation duration." Following the ejaculation, both male and female engaged in genital grooming behavior. Occasionally, male mice have been observed to bite the female's back at the end of the ejaculation period (McGill and Blight, 1963), but no instance of this behavior was recorded here. After a variable post-ejaculatory interval, the second copulatory series was initiated by the first mount with intromission, and ended with the second ejaculation.

B. Quantitative Results

Presented in Table I are the overall means obtained for 16 measures of mating behavior during first and second ejaculatory series, for both strains averaged across all tests. Given in Tables II and III are the results obtained in the three individual tests of copulatory behavior for the AKR/J and C3H/HeJ males respectively. An analysis of variance was performed for each of the

TABLE I
Overall Means for 16 Measures of Copulatory
Behavior of Nine AKR/J and Nine C3H/HeJ Male Mice
During First and Second Copulatory Series

	AKR/J		C3H/HeJ	
Measure	Series 1	Series 2	Series 1	Series 2
* ML	179.5		255.7	
* IL	233.5		376.2	
NM	8.66	8.56	12.96	5.96
NI	51.2	17.73	132.43	38.76
T/I	11.76	5.63	11.96	9.43
TNT	588.06	100.63	1577.6	395.76
NHM	1.8	0.5	4.0	1.46
* MTM	3.06	2.2	3.36	2.23
* MTI	8.8	4.96	14.5	11.73
% Bite	0.0	0.0	0.0	0.0
* MIII	62.5	132.0	51.2	68.4
* MPIMD	1.43	1.23	2.06	1.73
PET	15.36	11.8	21.93	19.1
* EL	2332.0	1876.96	7245.66	1958.8
* ED	14.2	12.4	25.6	23.56
* PEI	1369.7		2634.4	

* (All time measures are in seconds)

(For a key to abbreviations in this table see pp. 19-21)

TABLE II

Means for 16 Measures of Copulatory Behavior in Nine AKR/J Male Mice During
First and Second Copulatory Series, with Three Replications

Strain: AKR/J

	Test 1		Test 2		Test 3	
Measure	Series 1	Series 2	Series 1	Series 2	Series 1	Series 2
* ML	103.8		207.0		227.7	
* IL	168.1		259.8		272.6	
NM	7.9	5.9	9.8	11.6	8.3	8.2
NI	56.9	13.9	49.0	19.3	47.4	20.0
T/I	12.0	6.0	10.9	5.0	12.4	5.9
TNT	625.1	82.1	543.4	101.4	595.7	118.4
NHM	1.9	0.2	1.8	0.5	1.7	0.8
* MTM	3.1	1.9	3.1	2.4	3.0	2.3
* MTI	8.7	5.0	8.7	5.1	9.0	4.8
% Bite	0.0	0.0	0.0	0.0	0.0	0.0
* MIII	70.6	179.5	56.9	103.0	60.0	113.5
* MPIMD	1.2	1.1	1.7	1.3	1.4	1.3
PET	12.6	10.0	16.9	12.6	16.6	12.8

TABLE II (continued)

Measure	Test 1		Test 2		Test 3	
	Series 1	Series 2	Series 1	Series 2	Series 1	Series 2
* BL	3753.9	1490.9	3251.3	1977.3	3290.8	2162.7
* ED	13.7	12.4	15.0	12.5	13.9	12.3
* PEI	1332.2		1450.2		1326.7	

* (All time measures are in seconds)

(For a key to abbreviations in this table see pp. 19-21)

TABLE III

Means for 16 Measures of Copulatory Behavior
in Nine C3H/HeJ Male Mice During First and Second Copulatory
Series, with Three Replications

Strain: C3H/HeJ

Measure	Test 1		Test 2		Test 3	
	Series 1	Series 2	Series 1	Series 2	Series 1	Series 2
* ML	260.2		279.2		227.7	
* IL	346.7		411.8		370.1	
NM	13.4	6.0	11.2	6.0	14.3	5.9
NT	137.4	48.8	121.7	34.3	138.2	33.2
T/I	12.8	9.8	11.5	10.3	11.6	8.2
TNT	1757.8	489.4	1352.6	368.7	1622.4	329.2
NHM	5.1	1.2	3.7	1.8	3.2	1.4
* MTM	3.2	2.2	3.3	2.2	3.6	2.3
* MTI	14.7	10.7	14.1	10.8	14.7	13.7
% Bite	0.0	0.0	0.0	0.0	0.0	0.0
* MIII	51.8	40.7	52.1	74.2	49.7	90.3
* MPIMD	2.0	1.7	2.1	1.9	2.1	1.6
PET	21.1	16.0	20.8	18.1	23.9	23.2

TABLE III (continued)

Measure	Test 1		Test 2		Test 3	
	Series 1	Series 2	Series 1	Series 2	Series 1	Series 2
* EL	7515.0	2093.2	6640.2	1919.2	7581.8	1864.0
* ED	25.2	23.1	26.3	24.3	25.3	23.3
* PEI	2681.9		2589.0		2632.3	

* (All time measures are in seconds)

measures involved, and the complete ANOVA tables can be
found in Appendix I.

Although 64 males were used for the mating tests,
29 animals failed to mate and had ten successive "nega-
tive" tests, while 17 animals died during the experi-
ment. The data presented in Tables I-III were obtained
from the nine AKR/J and nine C3H/HeJ males which com-
pleted three "positive" mating tests.

Compared to the C3H/HeJ animals, the AKR/J males had
significantly shorter intromission latencies (IL), mean
times of intromission (MTI), mean pre-intromission mount
durations (MPIMD), ejaculation latencies (EL), ejacula-
tion durations (ED), and post-ejaculatory intervals (PEI).
They also had significantly fewer intromissions (NI),
thrusts (TNT), head mounts (NHM), and pre-ejaculatory
thrusts (PET). F ratios and significance levels for
these and other comparisons are given in Table IV.

The second series behavior for both strains was
characterized by a shortened ejaculation latency (EL)
and a reduced number of mounts (NM), intromissions (NI),
thrusts (TNT), head mounts (NHM), and thrusts per intro-
mission (T/I).

A significant interaction effect of strain x series
was found for the number of intromissions (NI), the to-
tal number of thrusts (TNT) and the ejaculation latency
(EL).

Significant decreases over tests were obtained for

TABLE IV

Obtained F Ratios for Main Effects and
Interaction for 15 Measures of Copulatory Behavior

Measure	A	B	C	AB	AC	BC	ABC
ML	2.00 a		1.04 b	1.60 a			
IL	6.38 *a		1.79 b	0.44 a			
NM	0.24 a	0.00 a	1.04 b	1.73 a	2.71 b	5.03 b	4.11 *b
NI	17.75 **a	29.24 **a	1.83 b	7.65 *a	4.02 *b	50.15 **b	11.01 **b
T/I	4.38 a	9.50 **a	2.76 b	0.29 a	2.36 b	17.21 **b	3.86 *b
TNT	13.16 **a	37.44 **a	8.31 **b	9.08 **a	5.70 **b	62.77 **b	10.51 **b
NHM	6.59 *a	5.36 *a	4.46 *b	1.93 a	2.35 b	15.91 **b	1.46 b
MTM	0.38 a	1.29 a	0.32 b	0.14 a	1.56 b	32.34 **b	0.48 b
MTI	23.86 **a	2.20 a	0.42 b	1.49 a	0.91 b	14.11 **b	0.92 b
MIII	3.36 a	0.18 a	0.11 b	1.17 a	1.90 b	3.70 *b	2.13 b
MPIMD	11.52 **a	0.07 a	0.45 b	0.64 a	1.98 b	6.23 **b	0.33 b
PET	15.92 **a	0.97 a	1.02 b	0.24 a	0.01 b	3.84 *b	0.93 b
EL	19.06 **a	24.73 **a	0.98 b	10.19 **a	2.11 b	134.22 **b	38.11 **b
ED	188.26 **a	3.39 a	0.92 b	0.09 a	0.31 b	0.88 **b	0.14 b
PEI	28.82 **a		0.26 b	1.88 a			

TABLE IV (continued)

(A = Strain; B = Series; C = Test)

a. $F_{.05} = 4.49$, $F_{.01} = 8.53$

b. $F_{.05} = 3.30$, $F_{.01} = 5.34$

* $p < .05$; ** $p < .01$

(For a key to abbreviations in this table see pp. 19-21)

the total number of thrusts (TNT) and the number of head mounts (NHM).

Significant interaction effects between strain and test were found for the number of intromissions (NI) and the total number of thrusts (TNT).

The interaction between series and test was found to be significant for all measures, except % bite. No male of either strain was observed to bite the female at the end of the ejaculation duration during any of the tests included in the present research.

The interaction of strain x series x test was found to be significant for the number of mounts (NM), the number of intromissions (NI), the number of thrusts per intromission (T/I), the total number of thrusts (TNT), and the ejaculation latency (EL).

The effect of changing the female following the first ejaculation is shown in Table V, in which are presented 16 measures of first and second series behavior under experimental (change of female) and control conditions. Overall, AKR/J males exhibited significantly shorter ejaculation latencies (EL), ejaculation durations (ED), and post-ejaculatory intervals (PEI), as well as a lower total number of thrusts (TNT) than their C3H counterparts. Table VI gives the F ratios and significance of these and other comparisons. The ANOVA tables are given in Appendix II.

Experimental males had significantly shorter mean times of mount (MTM), ejaculation latencies (EL), and

TABLE V

Means in Seconds and Mean Frequencies for 16 Measures
of Mating Behavior in First and Second Second Ejaculatory Series,
with and without Change of Female Following the First Ejaculation, for
Six AKR/J, and Six C3H/HeJ Male Inbred Mice

	Experimental				Control			
	Series 1		Series 2		Series 1		Series 2	
Measure	AKR/J	C3H/HeJ	AKR/J	C3H/HeJ	AKR/J	C3H/HeJ	AKR/J	C3H/HeJ
ML	222.7	226.5			125.5	221.8		
IL	402.5	370.5			281.0	333.8		
NM	6.5	13.5	0.5	1.8	8.7	17.0	5.2	6.0
NI	40.7	115.2	0.0	23.2	40.7	136.8	20.5	43.7
T/I	12.2	9.1	*	29.7	12.4	9.1	6.3	13.7
TNT	502.3	954.5	36.0	707.5	524.2	1183.5	133.2	667.8
NHM	1.3	2.7	0.2	0.0	3.5	4.3	1.0	2.0
MTM	2.8	2.2	0.3	2.2	3.8	2.8	2.3	2.3
MTI	9.2	8.0	*	22.7	8.8	8.5	5.0	8.5
% Bite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MIII	67.1	73.6	*	63.5	68.0	60.8	96.7	74.2
MPIMD	1.3	1.8	*	2.0	1.2	2.0	1.0	2.2

TABLE V (continued)

| Measure | Experimental | | | | Control | | | |
| | Series 1 | | Series 2 | | Series 1 | | Series 2 | |
	AKR/J	C3H/HeJ	AKR/J	C3H/HeJ	AKR/J	C3H/HeJ	AKR/J	C3H/HeJ
PET	18.3	22.0	36.0	31.7	15.7	21.0	11.8	20.7
EL	3009.0	7978.0	14.3	1864.0	3136.0	7541.7	1952.0	2721.2
ED	12.8	28.8	14.3	31.0	14.5	28.3	11.8	24.0
PEI	1007.0	3805.7			1422.7	3005.0		

(* Measure not applicable)

(For a key to abbreviations in this table see pp. 19-21)

TABLE VI

Obtained F Ratios for Main Effects and
Interaction in the Change of Female Tests

Measure	A	B	C	AB	AC	BC	ABC
ML	0.45	1.10		0.84			0.32
IL	0.01	1.45		0.42			
NM	8.92	16.86 **	80.24 **	0.05	13.44 **	0.94	0.32
NI	7.12	2.58	53.68 **	0.31	13.71 **	2.09	2.62
TNT	7.08	0.70	38.03 **	0.04	0.13	0.60	1.89
NHM	3.85	15.62 **	39.30 **	0.16	0.93	0.76	1.86
MTM	0.02	15.29 **	16.20 **	4.88	9.80 *	0.38	3.46
PET	1.43	20.01 **	4.08	2.92	0.15	10.31 **	1.37
EL	13.49 **	6.30 *	171.23 **	2.76	34.22 **	6.70 *	0.18
ED	39.66 **	11.55 **	0.44	7.39 *	0.04	8.04 *	0.38
PEI	5.25 *	2.62		0.04			

($F_{.05} = 4.96$, $F_{.01} = 10.04$)

(* $p < .05$; ** $p < .01$)

(A = Strain; B = Change of Female; C = Series)

(For a key to abbreviations in this table see pp. 19-21)

post-ejaculatory intervals (PEI), while at the same time
exhibiting longer ejaculation durations (ED), and per-
forming more pre-ejaculatory thrusts (PET), but fewer
mounts (NM) and head mounts (NHM) than the control ani-
mals.

When the behavior of experimental and control ani-
mals was compared across copulatory series, the second
series was characterized by significantly shorter mean
times of mount (MTM) and ejaculation latencies (EL), as
well as by fewer mounts (NM), intromissions (NI), thrusts
(TNT), and head mounts (NHM).

Significant interaction between strain and experi-
mental condition (change of female) was obtained for the
ejaculation duration (ED). Interaction between strain
and series was significant for the number of mounts (NM),
the number of intromissions (NI), the mean time of mount
(MTM), and the ejaculation latency (EL). The interaction
between series and experimental condition was significant
for pre-ejaculatory thrusts (PET), ejaculatory latency
(EL), and ejaculation duration (ED).

Out of the above, the main interaction effects were,
as expected, those between series and experimental condi-
tion. The behavior of AKR/J males during the second cop-
ulatory series, with change of female, was markedly dif-
ferent from that of the control AKR/J animals, and from
the second series behavior of experimental and control
C3H/HeJ males. Following the change of female, the second

series behavior of the albino males consisted of a single
mount with intromission, including a mean of 36 thrusts,
and ending in ejaculation after a mean ejaculation latency
of 14.3 seconds. By contrast, the experimental C3H/HeJ
males exhibited a mean of 23.2 intromissions, including
over 700 thrusts, and a mean ejaculation latency of 1864
seconds during their second copulatory series.

Presented in Table VII are t test values for indi-
vidual comparisons of experimental and control animals in
both strains. Significant t values were obtained for
several measures, when the second series behavior following
a change of female was compared with the behavior of the
control animals. The marked difference between AKR/J and
C3H/HeJ animals is apparent from an inspection of this
table. Number of intromissions (NI), thrusts per intro-
mission (T/I), mean time of intromission (MTI), mean inter-
intromission interval (MIII), and mean pre-intromission
mount duration (MPIMD) are not applicable due to the ab-
sence of intromissions during the second series behavior
of AKR/J males following the change of female.

Aggressive Behavior and the Interaction of Sex with Aggression

Inter-male aggression tests in AKR/J and C3H/HeJ males
were characterized by preliminary exploratory behavior,

TABLE VII
_t_ Test Values for Experimental and Control
Animals on 12 Measures of Mating Behavior

Measure	AKR/J		C3H/HeJ	
	Series 1	Series 2	Series 1	Series 2
ED	0.03	9.26**	0.28	1.94
NM	0.82	3.09*	1.51	3.34**
NI	0.00	11.85**	0.51	0.94
PET	0.83	3.38**	0.22	2.25*
TNT	0.28	9.12**	0.71	0.10
T/I	0.35	(a)	0.01	2.15
ED	2.00	2.68*	0.22	2.77*
NHM	2.14	1.55	1.71	3.85**
MTM	2.09	5.17**	1.91	0.19
MTI	0.32	(a)	0.38	2.78*
MIII	0.07	(a)	0.55	0.70
MPIMD	0.60	(a)	1.02	1.03s
PEI	4.10**		0.61	

$$t_{.05} = 2.23$$
$$t_{.01} = 3.17$$

(a) Not applicable

* p .05; ** p .01

(For a key to abbreviations in this table see pp. 19-21)

orienting, sniffing, and tail-thumping, usually followed
by a rapid attack which involved pushing, wrestling, and
biting the opponent. Often one male would lie on his back
while the other would climb on top of him. The mouse on
top was usually that regarded as the winner. If the de-
feated animal moved to escape, pursuit would often follow.

The AKR/J males initiated the first attack more
frequently, exhibited more instances of tail rattling, and
won more inter-strain bouts than their C3H/HeJ adversaries,
as can be seen in Table VIII. The AKR/J males also exhibi-
ted shorter attack latencies and scored higher in overall
aggression.

Total aggression scores (TSA), tail-rattling frequen-
cies (TR), first attack frequencies (FA), number of bouts
won (NW), and mean attack latencies (MAL) were compared
with each other and with the following measures of copula-
tory behavior: mating quotient (MQ), the ratio of positive
to negative mating tests, mean mount latency (ML), mean
intromission latency (IL), mean post-ejaculatory interval
(PEI), and mean ejaculation latencies for first and second
ejaculatory series (EL-1 and EL-2).

As was expected, the measures of aggressive behavior
included in the TSA (TR, FA, and NW) were found to corre-
late significantly with each other.

Significant correlations were also found among meas-
ures of copulatory behavior (Table IX). Mount latency (ML)
and intromission latency (IL) were correlated (r = 0.90),

TABLE VIII
Inter-Strain Bout Aggression Scores for
Two Inbred Strains of Mice

Strain	AKR/J n: 5	C3H/HeJ n: 9
Total Aggression Score (TSA)	22.60	3.77
Tail Rattling (TR)	6.20	0.55
First Attack (FA)	6.20	0.66
Number of Wins (NW)	6.00	0.77
Mean Attack Latency (MAL)	79.42	115.00

(TR, FA, and NW are in frequencies; MAL are in seconds)

TABLE IX

Correlation Coefficients for 11 Aggression and Mating Variables

Variables	1	2	3	4	5	6	7	8	9	10	11
1. TSA		.99*	.98*	.98*	-.33	-.08	.33	.19	-.55	-.54	.06
2. TR	.99*		.99*	.98*	-.35	-.10	.29	.13	-.58	-.58	.07
3. FA	.99*	.99*		.98*	-.32	-.10	.31	.16	-.57	-.57	.08
4. NW	.98*	.98*	.98*		-.30	-.04	.29	.12	-.57	-.57	.00
5. MAL	-.33	-.35	-.32	-.30		-.20	.10	.09	-.06	-.03	-.52
6. MQ	-.08	-.10	-.10	-.04	-.20		.13	.17	-.02	-.14	-.38
7. ML	.33	.29	.31	.29	.10	.13		.90*	.15	.25	-.05
8. IL	.19	.13	.16	.12	.09	.17	.90*		.32	.41	.03
9. PEI	-.55	-.58	-.57	-.57	-.06	-.02	.15	.32		.90*	.54
10. EL-1	-.54	-.58	-.57	-.57	-.03	-.14	.25	.41	.90*		.47
11. EL-2	.06	.07	.08	.00	-.52	-.38	-.05	.03	.54	.47	

(* Indicates a significant correlation)

(For a key to abbreviations in this table see pp. 19-22)

as were ejaculation latency for the first ejaculatory
series (EL-1) and post-ejaculatory interval (PEI)
(r = 0.90).

Nevertheless, no significant correlation was found
between measures of sexual behavior and measures of ag-
gression.

In order to examine the possibility of a within-strain
relationship of sexual and aggressive measures, t tests
were used to compare the four C3H/HeJ males scoring highest
in total aggression (TSA) with the four scoring lowest, in
terms of measures of copulatory behavior (Table X). The
measures of sexual behavior used were mount latency (ML),
intromission latency (IL), post-ejaculatory interval (PEI),
and ejaculation latencies (EL-1 and EL-2). These measures
were selected because they are related to the main aspects
of the theoretical models of sexual behavior discussed
above. No significant differences were found.

TABLE X

t Tests for Five Measures of Sexual Behavior
of Four C3H/HeJ Males with Highest Total Aggression
Scores (TSA) and Four C3H/HeJ Males with Lowest TSA

Measures	High TSA (Means)	Low TSA (Means)	t	p
ML	293.42	225.10	1.69	n.s.
IL	419.15	343.40	1.60	n.s.
PEI	2712.85	2442.75	0.51	n.s.
EL-1	7789.75	6625.75	0.82	n.s.
EL-2	2055.40	1671.47	0.72	n.s.

(For a key to abbreviations in this table see pp. 19-22)

DISCUSSION

The present research had five main objectives, which
will now be examined in terms of the obtained data.

The first objective was to describe the copulatory
behavior of AKR/J males during the first copulatory series,
and to compare such data with those of McGill and Ransom
(1968) in order to examine inter-laboratory variability.

A comparison of the present data on AKR/J mice with
those obtained by McGill and Ransom (1968) shows general
agreement on most, but not all, measures (Table XI). Dis-
crepancies were found in the number of mounts (NM), number
of intromissions (NI), total number of thrusts (TNT), mean
inter-intromission intervals (MIII), and ejaculation laten-
cies (EL). The observed inter-laboratory variability may
have been affected by any of several factors, such as the
receptivity of the stimulus females, the testing condi-
tions, and the scoring methods.

No measure of female receptivity was obtained in the
present study. The animals were tested in a different
locality, at a different time of the year, and using
slightly different testing environments.

The greatest discrepancy between the present data and
those of McGill and Ransom was in terms of the reported

TABLE XI
Median Scores for 16 Measures of the Copulatory
Behavior of Nine Male AKR/J Mice and Similar Data Obtained
by McGill and Ransom (1968)

AKR/J - Medians

Measure	McGill & Ransom, 1968	Test 1 Series 1	Test 1 Series 2	Test 2 Series 1	Test 2 Series 2	Test 3 Series 1	Test 3 Series 2
* ML	73	67		148		112	
* IL	190	122		210		140	
NM	55	7	6	10	6	8	5
NI	32	45	10	47	20	47	21
T/I	10	13	6	11	5	12	6
TNT	376	692	84	489	115	623	102
NHM	2	2	0	1	1	1	0
* MTM	2	3	2	3	2	3	2
* MTI	8	9	5	8	5	9	5
% Bite		0	0	0	0	0	0
* MIII	35	68	96	52	86	55	96
* MPIMD	1	1	1	2	1	1	1
PET	11	11	9	17	13	15	12

TABLE XI (continued)

Measure	McGill & Ransom 1968	Test 1		Test 2		Test 3	
		Series 1	Series 2	Series 1	Series 2	Series 1	Series 2
* EL	2160	3541	1380	3720	1832	3230	1993
* ED	13	14	13	14	12	15	12
* PEI		1260		1390		1270	

* (All time measures are in seconds)

(For a key to abbreviations in this table see pp. 19-21)

mount frequencies. The latter reported a median of 55 mounts, while a median of 8 was obtained in the present study. This may have been due in part to differences in scoring methods. For example, instances of a male climbing on the female were not recorded as "mounts" unless accompanied by pelvic thrusting without achieving intromission. Different observers are likely to disagree in borderline cases of weak pelvic movement.

The differences in ejaculation latencies are more difficult to interpret, although the median of 2160 seconds reported by McGill and Ransom falls well within the range for first-series EL reported in the present study (1380 to 5880 seconds).

The discrepancies found between the present data and those of McGill and Ransom suggest that normative data should be obtained for the different laboratories. Such data would facilitate meaningful comparisons between the results obtained by various investigators.

The second objective of the present study was to describe the copulatory behavior of the C3H/HeJ males. Compared to the AKR/J animals, the C3H/HeJ males exhibited longer latencies (ML, IL, EL), and more mounts, thrusts, and intromissions. Significant differences were also found in terms of the recovery of sex drive, measured by the post-ejaculatory interval (PEI). While no AKR/J male needed more than 2000 seconds for recovery (the mean PEI being 1369.7 seconds), only six times in 27 tests did a C3H/HeJ

male achieve an intromission within 2000 seconds following
the first ejaculation (mean: 2634.4 seconds). The six
instances in which the PEI was shorter than 2000 seconds
occurred in successive tests of the same two experimental
males. These data, as well as those presented by McGill
and Blight (1963) strongly suggest that recovery of sex
drive is dependent on the male mouse genotype.

A better appreciation of between-strain variability
in the copulatory behavior of different inbred strains of
Mus musculus can be obtained by comparing the present
results with those of previous studies. Since data re-
ported in terms of means are not directly comparable with
those reported as medians, two different tables were pre-
pared. In Tables XII and XIII are given the present re-
sults together with those of previous researches, given
in means and medians, respectively. The Levine, Barsel,
and Diakow (1966) data are not directly comparable with
those of McGill and his associates, not only because the
former reported means rather than medians, but because
their stimulus females were in natural estrus, while the
females used by McGill were in hormone-induced estrus.
The type of estrus may be an important factor in deter-
mining the mating pattern of ST and CBA males (Levine,
Barsel, and Diakow, 1966). Vale, Lee, and Ray (1970) and
Vale and Ray (1972) also reported means, while McGill and
his associates present their quantitative data in the form
of medians.

TABLE XII

A Comparison of Copulatory Behavior Measures of AKR/J and C3H/HeJ Males with That of Strains Reported in Other Studies

Measures	AKR/J	C57BL/6	C57BL/6J	A/J	DBA/2J	ST	CBA	C3H/HeJ
ML	179.5	309.9	147.5	541.1	96.6	390.0	300.0	255.7
IL	233.5	351.5	178.8	609.5	135.7	666.0	402.0	376.2
NM	8.7	30.8	27.1	12.2	34.8		23.0	13.0
NI	51.2	23.7	19.3	9.3	27.5	38.5	23.0	132.4
T/I	11.8					6.0	12.2	12.0
TNT	588.1	410.3	351.2	127.1	362.4	235.1	244.8	1577.6
NHM	1.8	1.4	3.0	1.9	1.6			4.0
MTM	3.1	2.0						3.4
MTI	8.8	15.4	13.1	13.7	10.7			15.4
% Bite	0.0	0.0	0.0			0.0	0.0	0.0
MIII	62.5	24.6	34.9	92.9	39.4			51.2
MFIMD	1.4							2.1
PET	15.4							21.9
EL	3432.0	1180.0	974.7	1351.3	1446.7	2352.0	1698.0	7245.7

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TABLE XII (continued)

Measures	AKR/J	C57BL/6	C57BL/6J	A/J	DBA/2J	ST	CBA	C3H/HeJ
ED	14.2	18.9	29.3	12.5	21.9			25.6
PEI	1369.7							2634.4
	(Mosig, 1974)	(Vale, Lee, and Ray, 1970)	(Vale and Ray, 1972)	(Vale and Ray, 1972)	(Vale and Ray, 1972)	(Levine, Barsel, and Diakow, 1960)	(Levine, Barsel, and Diakow, 1960)	(Mosig, 1974)

(All figures are means)

(Time measures are in seconds)

(For a key to abbreviations in this table see pp. 19-21)

TABLE XIII

A Comparison of Copulatory Behavior Measures
of the AKR/J and C3H/HeJ Strains with Strains
Reported by Other Authors

Measures	AKR/J	BALB/C	C57BL	C57BL/6J	DEA/2	DEA/2J	DBA/2J	C3H/HeJ
ML	112	62	29	42	68	85	56	274
IL	140	116	46	107	199	179	160	375
NM	8	18	10	18	15	16	12	12
NI	47	36	23	17	7	5	13	142
T/I	12	14	18	16	19	20	18	12
TNT	623	621	441	400	142	129	238	1435
NHM	1	5	2	2	0	0.5	0	4
MTM	3	2	2	2	5	7	5	3
MTI	9	12	15	15	18	20	17	17
% Bite	0	0	0	0	33	20	10	0
MIII	55	56	33	28	215	137	88	40
MPIMD	1	1	1	1	3	4	3	2
EL	3541	3645	1258	1252	1764	1376	1946	6943

TABLE XIII (continued)

Measures	AKR/J	BALB/C	C57BL	C57BL/6J	DBA/2	DBA/2J	DBA/2J	C3H/HeJ
ED	14	13	19	23	19	17	20	25
	(Mosig, 1974)	(McGill, 1962)	(McGill, 1962)	(McGill and Blight, 1963)	(McGill, 1962)	(McGill and Blight, 1963)	(McGill and Ransom, 1968)	(Mosig, 1974)

(All figures are medians)

(Time measures are in seconds)

(For a key to abbreviations in this table see pp. 19-21)

In addition to genotype, it is possible that the differences apparent in Tables XII and XIII are due in part to within-strain and inter-laboratory variabilities.

The AKR/J animals had relatively shorter mount latencies (ML), intromission latencies (IL), mean times of intromission (MTI), and ejaculation durations (ED) than the ST, CBA, C57BL and A/J males (Table XII). The AKR/J males also exhibited fewer mounts and more intromissions and thrusts than the mentioned strains. On the other hand, the C3H/HeJ males, exhibited an extraordinarily high number of intromissions and thrusts, and the longest ejaculation latencies recorded.

Table XIII shows that the AKR/J males resembled the BALB/c males tested by McGill (1962) in the total number of thrusts (TNT), the mean inter-intromission interval (MIII), the ejaculation latency (EL), the ejaculation duration (ED), and the lack of post-ejaculatory biting behavior (% bite), the latter being a behavior reported on this table only for the DBA animals. The albino males also exhibited relatively longer mount latencies, (ML), shorter mean time of intromission (MTI), fewer mounts (NM) and thrusts per intromissions (T/I), but more intromission (NI) than the other strains. On the other hand, the C3H/HeJ males again exhibited the longest mount and intromission latencies (ML and IL), ejaculation latencies (EL), and ejaculation durations (ED), as well as the highest number of intromissions (NI) and thrusts (TNT)

recorded, although they were similar to the other strains
on the table in terms of the number of mounts (NM),
thrusts per intromission (T/I), mean time of mount (MTM),
and mean time of intromission (MTI). Their mean inter-
intromission intervals (MIII) resembled those of the C57
animals, and they lacked post-ejaculatory biting behavior,
like the AKR, C57, and BALB males.

C3H/HeJ mice are the slowest copulating strain ever
studied. Such an extremely slow behavior pattern, neces-
sitating a mean of slightly over two hours to achieve a
single ejaculation, would be likely to have a detrimental
effect on the animal's reproductive success in the wild.
It is hard to imagine that this behavior could have adapt-
ive value for the animal or the species. The slow behavior
pattern of C3H/HeJ mice is probably an artifact of the pro-
cess of inbreeding, and it is not likely that such behavior
is found in the wild.

The third objective of the present research was to
provide the first data regarding copulatory behavior of
AKR/J and C3H/HeJ mice during the second series, and
relate the data to the theoretical models of sex be-
havior. The second series behavior of both strains
was characterized by a greatly reduced number of intro-
missions (NI), thrusts (TNT), and head mounts (NHM)
and shorter ejaculation latencies (EL). Although
animals of both strains also exhibited shorter mean
times of intromission (MTI), mean pre-intromission

mount durations (MPIMD), and ejaculation durations
(ED), as well as longer inter-intromission intervals (III),
these differences failed to reach significance. These
results are similar to those obtained for rats by Larsson
(1956) and Beach and Jordan (1956).

The obtained second series data are compatible with
the models of sexual behavior reviewed in the Introduction.
According to Beach (1956) and McGill (1965) the effect of
the first ejaculatory series and first ejaculation on the
behavior during the second series is one of sensitization
of the arousal (AM) and copulatory (CM) mechanisms. The
present data support these theoretical views, and the sen-
sitizing effect of the first copulatory series is reflected
in the lower number of thrusts and intromissions, and
shorter ejaculation latencies, needed to reach the thresh-
old for the second ejaculation.

Nevertheless, the significant correlation found be-
tween post-ejaculatory interval (PEI) and ejaculation
latency (EL-1) would not have been predicted by the McGill
model. According to the three-mechanism theory, the ejacu-
lation discharges an ejaculatory mechanism (EM), and a cer-
tain minimum recovery of the EM must take place before
copulation can resume. The recovery of the EM is measured
by the PEI, and is dependent on the genotype. The ejacu-
lation latency (EL), on the other hand, measures the cop-
ulatory mechanism (CM). If the EL and the PEI measure two
different mechanisms, a high correlation between the two

would not be expected. The present data appear to support the dual mechanism theory. If the EL correlates highly with the PEI, it is likely that both are measuring the same mechanism (CM).

The fourth major objective of the present research was to determine the effect of a change of female partner between copulatory series. The data presented in Table V clearly indicate that the effects of this variable varied with the genotype. After a post-ejaculatory interval (PEI) significantly shorter than that of the control animals, the experimental AKR/J males ejaculated in a single mount with intromission, with a mean of 36 pre-ejaculatory thrusts. The experimental C3H/HeJ animals, on the other hand, showed significantly fewer mounts, head mounts, and pre-ejaculatory thrusts than the controls, following the change of female, but required a mean of 23 intromissions before achieving the second ejaculation.

A reduction of the PEI was observed in both strains following the change of female, although in the case of the C3H males the difference was not statistically significant. Several C3H males attempted several mounts before achieving the first intromission of the second series with the unmated stimulus female. It is possible that differences in the receptivity of the new females may have affected the length of the PEI in these cases.

Since the experimental manipulation resulted in a shortening of the PEI, it could be hypothesized that the

fresh female introduced after the first ejaculation acted
as a novel stimulus, counteracting habituation to a con-
stant sexual stimulus, namely the original female. The
length of the PEI appears to depend not only on a minimum
necessary recovery of the EM, as suggested by McGill
(1965), but also on habituation. The reduction of the PEI
following the presentation of the fresh female argues
against the hypothesis that the PEI duration is dependent
on non-sexual fatigue effects (Beach & Whalen, 1959), be-
cause it seems unlikely that the novel sexual stimulus had
any effect on non-sexual fatigue. Instead, the novel
stimulus appears to counteract the habituation component
of sexual satiety.

The change of female also resulted in reduced second
series ejaculation latency (EL-2) and a general accelera-
tion of copulatory behavior with an increase in the number
of pre-ejaculatory thrusts needed to reach the ejaculatory
threshold. This indicates that the novel stimulus also
acts to further sensitize the AM and the CM.

It is tempting to speculate on the adaptive value of
habituation to a constant sex stimulus, and the releasing
or recuperative effect of a novel stimulus. Once the first
ejaculation has taken place, greater reproductive success,
as measured by the number of offspring sired, is more
likely to result from mating with a different female,
rather than with the original one, which would tend to in-
crease the frequency of the male's genotype in the gene
pool of the population.

On the other hand, greater reproductive success would not result from mating with a different female, if the male's sperm were displaced by the sperm of other males mating with the first female. Sperm competition has been demonstrated in insects (Parker, 1970) but the possible presence of this phenomenon in mice has not been established.

The habituation hypothesis of sexual satiety has been challenged by several studies. Tiefer (1969) and Dewsbury (1968), for instance, failed to elicit a greater amount of copulatory behavior in the male rat in multiple-female exhaustion tests. According to Tiefer, the rat's behavior follows an interval program regardless of the number of female partners, and the change in the male's behavior resulting from the introduction of a new partner may be due to some property or behavior of the fresh female. Dewsbury's data suggest that some factor acts to depress the CM in the male rat at satiety, whether or not the female was changed after each ejaculation by the male. Nonsexual fatigue and other more specific factors may be involved in the cessation of copulation in the rat. The present data suggest a fundamental difference between the factors affecting satiety in the male mouse and those active in the rat.

The present results resemble somewhat those obtained in the "Coolidge effect" with rats (Beach and Ransom, 1967; Fisher, 1962; Fowler and Whalen, 1961) although several

important differences in procedure should be noted. In a "Coolidge effect" experiment, the female is changed after a satiety criterion has been met, while in the present experiment, the female substitution followed the first ejaculation, a fundamentally different procedure, since our data, as well as those of previous studies, indicate that sexual satiety in the male mouse is not reached with the first ejaculation.

The present data show that there are significant strain differences in most measures of mating behavior, as well as in the effect of the change of female following the first ejaculation. It is interesting to speculate on the adaptive value of such differences in mating behavior. It would seem that a faster mating pattern would prove advantageous in a natural situation, since a shorter ejaculation latency would increase the probability of the transmission of sperm to the female, and at the same time reduce the interval during which the animal might be most vulnerable to predators. If there has been selective pressure toward faster mating patterns with reduced mount and intromission frequencies, why was the copulatory behavior of mice not reduced to a single mount with ejaculation? That such behavior is possible is shown by the second series behavior of AKR/J males following change of female.

In the case of rats, it has been suggested that it would not be adaptive for the male to minimize the number of intromissions preceding ejaculation, because, in addi-

tion to sperm transfer, several vaginal intromissions appear necessary for the induction of neuroendocrine reflexes essential for pregnancy and for sperm transport (Wilson, Adler, and LeBoeuf, 1965; Adler, 1969; Adler, Resko, and Goy, 1970; Chester and Zucker, 1970; Dewsbury, 1972).

On the other hand, the literature on the effects of male copulatory behavior on female pregnancy in Mus musculus suggests fundamentally different conclusions than the ones for Rattus norvegicus. Land and McGill (1967) found that a large number of pre-ejaculatory thrusts is neither necessary, nor sufficient, for the induction of luteal activity in the female mouse, and that the ejaculatory reflex and formation of the copulatory plug were sufficient stimuli regardless of the number of pre-ejaculatory thrusts. The suggested fundamental difference between the physico-endocrinological relationships of the rat and the mouse is also reflected in the failure to achieve pseudopregnancy following electrical and mechanical stimulation of the cervix of the mouse (Stone and Emmens, 1964; Finn, 1965), while several studies have shown that cervical stimulation of the rat results in pseudopregnancy (Nalbandov, 1964).

Nevertheless, Diamond (1970) used different patterns of mechanical stimulation to mimic normal vaginal stimulation during copulation, and concluded that the number and rate of intromissions were crucial in the induction

of pseudopregnancy, which can be taken as an indicator of
reproductive success. Diamond postulated a species-related
vaginal code with an optimal combination of penile inser-
tions and intervals between insertions, which would maxi-
mize the chances for reproductive success between conspe-
cifics. Some neural mechanism would be involved in the
integration of several variables (insertion number, rate
of insertion, total exposure time, duration of each inser-
tion, and others) to affect the neuroendocrine reflexes
necessary for pregnancy. Furthermore, Diamond suggested
that, given sufficient stimulation appropriate to the
species-related vaginal code, the ejaculatory reflex would
not be necessary for the induction of luteal activity, and
that contrary to the findings of Land and McGill (1967)
the number of intromissions should be considered as an
important variable.

McGill, Corwin, and Harrison, (1968) demonstrated that
pregnancy and pseudopregnancy resulted from mating with
males surgically rendered unable to form copulatory plugs,
and McGill and Coughlin (1970) determined that the stimulus
inducing luteal activity in the female mouse is the vaginal
stretching resulting from the swelling of the penis, which
normally precedes the release of the copulatory plug.
These findings were further confirmed by McGill (1970), who
found that the presence of the copulatory plug in the va-
gina is not necessary for the induction of luteal activity.
Pre-ejaculatory intromissions are not sufficient for in-

ducing luteal activity in female rats (Ball, 1934) or mice
(McGill, 1970; Land and McGill, 1967), but appear to be
necessary for successful pregnancy in the rat (Wilson,
Adler, and LeBoeuf, 1965). McGill (1970) concluded that
if a minimum number of intromissions is also necessary in
female mice, it is less than that required for female rats.

The present data indicate that AKR/J males can
achieve ejaculation within a single mount with repeated
intromittive thrusts and suggest that, at least in a case
where a novel sexual stimulus acts to counteract habitua-
tion and/or to further sensitize the CM, several mounts
with intromission are not necessary for the ejaculation,
although a number of pre-ejaculatory thrusts are required
to reach the ejaculation threshold. Future research is
needed to determine whether successful pregnancy or
pseudopregnancy is likely to result from the single mount-
with-ejaculation pattern of AKR/J males following a change
of female partner. Such research should help to determine
the relative importance of the species-related vaginal
code vs. the penile swelling during the ejaculatory reflex
in triggering luteal activity in the female mouse.

Dewsbury (1972) has suggested that the copulatory
behavior of male mammals be classified according to sixteen
different patterns, characterized by the presence or ab-
sence of locks, thrustings, multiple intromissions, and
multiple ejaculations. Within this scheme, the copulatory
behavior of Mus musculus was classified in the pattern

characterized by the absence of lock, and the presence of thrustings, multiple intromissions, and multiple ejaculations. The present data indicate that the laboratory mouse does not necessarily require multiple intromissions in order to achieve ejaculation. Following a change of stimulus female, AKR/J males achieve a second ejaculation within a single intromission with multiple thrustings. This important characteristic is reported here for the first time, and requires a change in the classification of the copulatory behavior of Mus musculus, unless the classification is considered to apply only to the normal copulatory pattern with a single female. In addition to a pattern characterized by the absence of lock and the presence of thrustings, multiple intromissions and multiple ejaculations (Pattern No. 9), the laboratory mouse can exhibit Pattern No. 11, with no lock or multiple intromissions, but with thrustings and multiple ejaculations.

Mus musculus is not the only species of Rodentia where ejaculations within a single penile insertion have been reported. For example, the guinea pig, Cavia porcellus (Young and Grunt, 1951); the California mouse, Peromyscus californicus (Dewsbury, in press); the southern grasshopper mouse, Onychomys torridus (Dewsbury and Jansen, 1972); the golden mouse, Ochrotomys nuttalli (Dewsbury, in press); the meadow vole, Microtus pennsylvanicus (Gray and Dewsbury, in preparation); the ground squirrel, Citellus richardsonii (Denniston, 1957); and the chinchilla, Chinchilla lanigera

(Bignami and Beach, 1968), all have been reported to ex-
hibit ejaculations within a single mount with intromission.
Nevertheless, there are many species in which ejaculation
has never been reported to occur on the first intromission.
The presence or absence of the capacity to achieve ejacu-
lation on the first mount with vaginal penetration has been
proposed as a major differentiating attribute of patterns
of copulatory behavior (Dewsbury, 1972). For this reason,
the present data indicating that the laboratory mouse _Mus
musculus_ can attain ejaculation in the first mount with
intromission are particularly significant.

The fifth objective of the present research was to
search for a correlation between quantitative measures of
aggressive behavior and measures of copulatory behavior.
Such correlation was not found.

The present data appear to indicate that aggressive
behavior in AKR/J and C3H/HeJ males is related to the
genotype. The AKR/J males were more aggressive than their
C3H counterparts, both in intra-strain and inter-strain
bouts, winning over 60% of their bouts with the C3H/HeJ
males. Their superiority would have been even more marked
than is apparent from Table IX, if data for one of the
AKR/J males, which did not fight at all, appeared sick,
and died shortly after the tests were terminated, had been
discarded. The observed superiority of AKR/J males over
C3H/HeJ males in inter-strain bouts is in agreement with
with the data reported by Southwick and Clark (1966).

Although the AKR/J animals were superior in aggressiveness as well as in mating speed, no correlation was found between measures of aggressive and copulatory behaviors. Nevertheless, these data cannot be regarded as being in direct contradiction to the findings of Levine, Barsel, and Diakow (1965), who reported an interaction of sexual and aggressive behaviors in male mice. Levine et al. worked with ST and CBA mice; their aggressive bouts were allowed to continue for one hour, and the males were fought in the presence of an estrous female. The situations were quite different from those in the present study, as were the dependent variables considered, and consequently there can be few meaningful comparisons.

The failure to find a relationship between sex and aggression in the present study may have been a function of the particular strains used, and it is possible that an interaction effect may be more readily observable when animals of other genetic backgrounds are compared.

The present data do not rule out the possbility that aggression may be related to reproductive superiority, since reproductive success is measured in terms of siring young, rather than in terms of temporal and quantitative aspects of the copulatory pattern. A comparison of success in a series of rather brief aggressive bouts, with copulatory vigor, as measured by diverse mating latencies and behavioral frequencies, can be misleading, since it fails to consider the actual reproductive success of the

animals in terms of litter size, frequencies of successful inseminations and pregnancies, and viability or survival ratios of the young.

A comparison of an animal's position in a dominance hierarchy, with his reproductive success in a competitive situation, would have been a more meaningful one, and more likely to have produced a significant correlation (Uhrich, 1938). Nevertheless, the greater reproductive success of a dominant animal cannot be regarded as a function of genotype alone, but as the result of the interaction of the genotype with environmental factors. For instance, the larger number of spontaneous ejaculations and greater mating success of dominant guinea pigs were found to be the outcome of differences in early social experience (Martan, 1968).

The aggressiveness observed in laboratory bouts may be an artifact of the testing situation, rather than an accurate reflection of fighting behavior occurring in a natural setting. Semi-natural studies, like those by Crowcroft and Rowe (1963) and others, suggest that little actual fighting occurs in stable populations. If this is the case, measures of fighting success in laboratory bouts may be rather artificial and poor indicators of genotype-linked aggressiveness.

Nevertheless, Scudder, Richardson, and Karczmar (1969) showed that when three genera of wild mice were compared with three strains of Mus musculus, the latter were supe-

rior in aggressiveness, exploratory behavior, and sexual behavior. Among the Mus musculus strains, the wild Mus musculus "Missouri" was superior in the three behavioral categories. Apparently wild house mice are equal or superior in aggressiveness to their inbred counterparts, although in the Scudder et al. study, all measures were obtained in an artificial "mouse city." This circumstance makes it impossible to discard the possibility that the aggressive behavior of Mus musculus "Missouri" resulted from an interaction of the wild genotypes with the experimental situation, and that such behavior would not have occurred in a natural setting. The failure to find a relationship between laboratory-induced aggression and copulatory behavior does not permit drawing any conclusion about a possible interaction in the field.

The process of domestication and inbreeding is also likely to have obscured any interaction between wild genotypes. For instance, laboratory animals are selected for high reproductive rates and survival in small cages, and certain aggressive behavior patterns, such as biting the experimenter, have been selected against.

There are several reasons why a relationship between sex and aggression could be expected in a natural setting. In the first place, it is undeniable that aggressiveness is frequently sex-dependent. Generally, low aggression, independently of the level of exploratory activity, characterizes the females of various strains (Karczmar and

Scudder, 1967). In addition, it is obvious that increased aggressiveness will tend to give a male access to more females in a competitive situation (Alverdes, 1935; Carpenter, 1942). Nevertheless, increased aggressiveness is not necessarily advantageous in terms of individual survival, unless it is goal-directed. This is apparently not the case in the highly aggressive, but non-competitive Mus strains (Scudder, Richardson, and Karczmar, 1969). In the Scudder et al. study, mice were fighting constantly, and the animals often suffered severe injuries and did not survive the longer experiments. It is possible that such a high level of aggressiveness may have been an artifact of the experimental situation.

In conclusion, although the present study did not find a significant relationship between measures of copulatory and aggressive behavior, it is likely that such relationship will appear when a more meaningful comparison is made between reproductive success and social dominance, or goal-directed aggression, in the behavior of wild Mus musculus in a natural setting.

APPENDIX I

Analyses of Variance for
15 Measures of Copulatory
Behavior in AKR/J and C3H/HeJ
Male Mice, During First
and Second Copulatory Series

ANOVA 1

Mount Latency (ML)

Source	SS	df	MS	F	p
Between Subj.		17			
A	77976.00	1	77976.00	2.00	n.s.
SWG	622915.00	16	38932.19		
Within Subj.		36			
B	36231.19	2	18115.59	1.04	n.s.
AB	55635.75	2	27817.88	1.60	n.s.
B x SWG	557111.00	32	17409.72		

ANOVA 2

Mount Latency (ML)

Source	SS	df	MS	F	p
Between Subj.		17			
A	274916.81	1	274916.81	6.38	<.05
SWG	689674.00	16	43104.63		
Within Subj.		36			
B	62649.00	2	31324.50	1.79	n.s.
AB	15348.38	2	7674.19	0.44	n.s.
B x SWG	558769.00	32	17461.53		

ANOVA 3

Number of Mounts (NM)

Source	SS	df	MS	F	p
Total	4492.77	107			
Between Subj.	1397.60	17			
A	20.45	1	20.45	0.23	n.s.
SWG	1377.15	16	86.07		
Within Subj.	3095.17	90			
B	0.01	1	.01	0.00	n.s.
AB	60.76	1	60.76	1.74	n.s.
B x SWG	559.06	16	34.94		
C	25.02	2	12.51	1.04	n.s.
AC	65.36	2	32.68	2.71	n.s.
C x SWG	385.30	32	12.04		
BC	400.24	2	200.12	5.03	$<.05$
ABC	327.16	2	163.58	4.11	$<.05$
BC x SWG	1272.28	32	39.76		

ANOVA 4

Number of Intromissions (NI)

Source	SS	df	MS	F	p
Total	317356.00	107			
Between Subj.	134490.63	17			
A	70737.87	1	70737.87	17.75	<.01
SWG	63752.75	16	3984.55		
Within Subj.	182865.37	90			
B	13691.25	1	13691.25	29.24	<.01
AB	3582.25	1	3582.25	7.65	<.05
B x SWG	7492.12	1	468.26		
C	884.25	2	442.12	1.84	n.s.
AC	1936.75	2	968.38	4.02	<.05
C x SWG	7709.38	32	240.92		
BC	95904.69	2	47952.34	50.15	<.01
ABC	21065.87	2	10532.94	11.02	<.01
BC x SWG	30598.81	32	956.21		

ANOVA 5

Thrusts per Intromission (T/I)

Source	SS	df	MS	F	p
Total	1782.52	107			
Between Subj.	504.07	17			
A	108.41	1	108.40	4.38	n.s.
SWG	395.66	16	24.73		
Within Subj.	1278.45	90			
B	69.85	1	69.85	9.50	<.01
AB	2.12	1	2.12	0.29	n.s.
B x SWG	117.59	16	7.35		
C	18.18	2	9.09	2.76	n.s.
AC	15.60	2	7.80	2.36	n.s.
C x SWG	105.56	32	3.30		
BC	440.78	2	220.39	17.21	<.01
ABC	98.90	2	49.45	3.86	<.05
BC x SWG	409.86	32	12.81		

ANOVA 6

Total Number of Thrusts (TNT)

Source	SS	df	MS	F	p
Total	53578160.00	107			
Between Subj.	24683440.00	17			
A	11139360.00	1	11140005.80	13.16	<.01
SWG	13544080.00	16	846505.00		
Within Subj.	28894720.00	90			
B	2204784.00	1	2204804.16	37.44	<.01
AB	534640.00	1	534640.00	9.08	<.01
B x SWG	942224.00	16	58889.00		
C	346752.00	2	173376.00	8.31	<.01
AC	237840.00	2	118920.00	5.70	<.01
C x SWG	667936.00	32	20873.00		
BC	16847152.00	2	8422855.22	62.78	<.01
ABC	2819440.00	2	1410294.86	10.51	<.01
BC x SWG	4293952.00	32	134186.00		

ANOVA 7

Number of Head Mounts (NHM)

Source	SS	df	MS	F	p
Total	527.67	107			
Between Subj.	234.67	17			
A	68.48	1	68.48	6.59	<.05
SWG	166.17	16	10.39		
Within Subj.	293.00	90			
B	14.81	1	14.82	5.36	<.05
AB	5.33	1	5.33	1.93	n.s.
B x SWG	44.18	16	2.76		
C	10.17	2	5.08	4.46	<.05
AC	5.35	2	2.68	2.35	n.s.
C x SWG	36.48	32	1.14		
BC	84.24	2	42.12	15.91	<.01
ABC	7.72	2	3.86	1.46	n.s.
BC x SWG	84.70	32	2.65		

ANOVA 8

Mean Time of Mount (MTM)

Source	SS	df	MS	F	p
Total	95.21	107			
Between Subj.	32.38	17			
A	0.75	1	0.75	0.38	n.s.
SWG	31.63	16	1.98		
Within Subj.	62.83	90			
B	0.75	1	0.75	1.29	n.s.
AB	0.08	1	0.08	0.14	n.s.
B x SWG	9.33	16	0.58		
C	0.24	2	0.12	0.32	n.s.
AC	1.17	2	0.58	1.56	n.s.
C x SWG	11.93	32	0.37		
BC	26.06	2	13.03	32.34	<.01
ABC	0.39	2	0.20	0.48	n.s.
BC x SWG	12.89	32	0.40		

ANOVA 9

Mean Time of Intromission (MTI)

Source	SS	df	MS	F	p
Total	2733.96	107			
Between Subj.	1746.30	17			
A	1045.33	1	1045.33	23.86	⩽.01
SWG	700.96	16	43.81		
Within Subj.	987.67	90			
B	10.70	1	10.70	2.20	n.s.
AB	7.25	1	7.25	1.49	n.s.
B x SWG	77.68	16	4.86		
C	5.68	2	2.84	0.42	n.s.
AC	12.17	2	6.08	0.91	n.s.
C x SWG	213.82	32	6.68		
BC	300.24	2	150.12	14.11	⩽.01
ABC	19.69	2	9.85	0.92	n.s.
BC x SWG	340.43	32	10.64		

ANOVA 10

Mean Inter-Intromission Interval (MIII)

Source	SS	df	MS	F	p
Total	824348.38	107			
Between Subj.	218498.88	17			
A	37911.44	1	37911.44	3.36	n.s.
SWG	180587.44	16	11286.72		
Within Subj.	605849.50	90			
B	1148.56	1	1148.56	0.18	n.s.
AB	7513.19	1	7513.19	1.17	n.s.
B x SWG	102869.56	16	6429.35		
C	1058.56	2	529.28	0.10	n.s.
AC	19008.75	2	9504.38	1.90	n.s.
C x SWG	160238.19	32	5007.44		
BC	53254.06	2	26627.03	3.70	<.05
ABC	30655.62	2	15327.81	2.13	n.s.
BC x SWG	230103.00	32	7190.72		

ANOVA 11

Mean Pre-Intromission Mount Duration (MPIMD)

Source	SS	df	MS	F	p
Total	37.44	107			
Between Subj.	18.60	17			
A	7.79	1	7.79	11.52	<.01
SWG	10.81	16	0.68		
Within Subj.	18.83	90			
B	0.01	1	0.01	0.07	n.s.
AB	0.08	1	0.08	0.64	n.s.
B x SWG	2.07	16	0.13		
C	0.13	2	0.06	0.45	n.s.
AC	0.57	2	0.29	1.98	n.s.
C x SWG	4.63	32	0.14		
BC	3.13	2	1.56	6.23	<.01
ABC	0.17	2	0.08	0.33	n.s.
BC x SWG	8.04	32	0.25		

ANOVA 12

Pre-Ejaculatory Thrusts (PET)

Source	SS	df	MS	F	p
Total	7985.86	107			
Between Subj.	2624.86	17			
A	1309.04	1	1309.04	15.92	<.01
SWG	1315.82	16	82.24		
Within Subj.	5361.00	90			
B	71.70	1	71.70	0.97	n.s.
AB	17.92	1	17.92	0.24	n.s.
B x SWG	1177.34	16	73.58		
C	107.80	2	53.90	1.02	n.s.
AC	1.24	2	0.62	0.01	n.s.
C x SWG	1688.96	32	52.78		
BC	424.24	2	212.12	3.84	<.05
ABC	103.02	2	51.51	0.93	n.s.
BC x SWG	1768.77	32	55.27		

ANOVA 13

Ejaculation Latency (EL)

Source	SS	df	MS	F	p
Total		107			
Between Subj.	188418610.56	17			
A	102431794.56	1	102431794.56	19.06	<.01
SWG	85986816.00	16	5374175.00		
Within Subj.	498980352.00	90			
B	26541312.00	1	26541312.00	24.73	<.01
AB	10932736.00	1	10932736.00	10.19	<.01
B x SWG	17171968.00	16	1073248.00		
C	1760768.00	2	880384.00	0.98	n.s.
AC	1891072.00	2	1891072.00	2.11	n.s.
C x SWG	28623616.00	32	894488.00		
BC	292184320.00	2	146092160.00	134.22	<.01
ABC	83005808.00	2	41547904.00	38.11	<.01
BC x SWG	34887680.00	32	1090240.00		

ANOVA 14

Ejaculation Duration (ED)

Source	SS	df	MS	F	p
Total	4173.86	107			
Between Subj.	3738.19	17			
A	3445.37	1	3445.37	188.26	<.01
SWG	292.82	16	18.30		
Within Subj.	435.67	90			
B	12.00	1	12.00	3.39	n.s.
AB	0.33	1	0.33	0.09	n.s.
B x SWG	56.64	16	3.54		
C	5.57	2	2.79	0.92	n.s.
AC	1.90	2	0.95	0.31	n.s.
C x SWG	97.19	32	3.04		
BC	99.50	2	49.75	9.88	<.01
ABC	1.40	2	0.70	0.14	n.s.
BC x SWG	161.13	32	5.04		

ANOVA 15

Post-Ejaculatory Interval (PEI)

Source	SS	df	MS	F	p
Between Subj.		17			
A	21594191.96	1	21594191.96	28.82	<.01
SWG	11988448.00	16	749278.00		
Within Subj.		36			
B	15264.00	2	7632.00	0.26	n.s.
AB	111456.00	2	55728.00	1.88	n.s.
B x SWG	949472.00	32	29671.00		

APPENDIX II

Analyses of Variance for
11 Measures of Copulatory
Behavior in AKR/J and C3H/HeJ
Male Mice, with a Change of
Female Following the First Ejaculation

ANOVA 16

Mount Latency (ML) with Change of Female

Source	SS	df	MS	F	p
Between Subj.		11			
A	8029.88	1	8029.88	0.45	n.s.
SWG	177424.63	10	17742.46		
Within Subj.		12			
B	8400.00	1	8400.00	1.10	n.s.
AB	6436.13	1	6436.13	0.84	n.s.
B x SWG	76426.63	10	7642.66		

ANOVA 17

Intromission Latency (IL) with Change of Female

Source	SS	df	MS	F	p
Between Subj.		11			
A	651.00	1	651.00	0.01	n.s.
SWG	683369.00	10	68336.88		
Within Subj.		12			
B	37525.13	1	37525.13	1.45	n.s.
AB	10795.13	1	10795.13	0.42	n.s.
B x SWG	258352.00	10	25835.20		

ANOVA 18

Number of Mounts (NM) with Change of Female

Source	SS	df	MS	F	p
Total	1831.48	47			
Between Subj.	487.23	11			
A	229.69	1	229.69	8.92	< .05
SWG	257.54	10	25.76		
Within Subj.	1344.25	36			
B	157.69	1	157.69	16.86	< .01
AB	0.52	1	0.52	0.06	n.s.
B x SWG	93.54	10	9.35		
C	776.02	1	776.02	80.24	< .01
AC	130.02	1	130.02	13.44	< .01
C x SWG	96.71	10	9.67		
BC	7.52	1	7.52	0.94	n.s.
ABC	2.52	1	2.52	0.32	n.s.
BC x SWG	79.71	10	7.97		

ANOVA 19

Number of Intromissions (NI) with Change of Female

Source	SS	df	MS	F	p
Total	167009.69	47			
Between Subj.	84897.19	11			
A	35316.69	1	35316.69	7.12	<.05
SWG	49580.50	10	4958.05		
Within Subj.	82112.50	36			
B	2945.31	1	2945.31	2.58	n.s.
AB	352.12	1	352.12	0.31	n.s.
B x SWG	11406.06	10	1140.61		
C	45386.94	1	45386.94	53.68	<.01
AC	11594.19	1	11594.19	13.71	<.01
C x SWG	8454.38	10	845.44		
BC	280.38	1	280.38	2.09	n.s.
ABC	351.81	1	351.81	2.62	n.s.
BC x SWG	1341.31	10	134.13		

ANOVA 20

Total Number of Thrusts (TNT) with Change of Female

Source	SS	df	MS	F	p
Total	13887984	47			
Between	9716640	11			
A	4028672	1	4028672.00	7.08	<.05
SWG	5687968	10	568796.75		
Within Subj.	4171344	36			
B	71304	1	71304.00	0.70	n.s.
AB	3720	1	3720.00	0.04	n.s.
B x SWG	1018096	10	101809.56		
C	1968288	1	1968288.00	38.03	<.01
AC	6720	1	6720.00	0.13	n.s.
C x SWG	517504	10	51750.40		
BC	28040	1	28040.00	0.60	n.s.
ABC	88728	1	88728.00	1.89	n.s.
BC x SWG	468944	10	46894.40		

ANOVA 21

Number of Head Mounts (NHM) with Change of Female

Source	SS	df	MS	F	p
Total	165.25	47			
Between Subj.	24.25	11			
A	6.75	1	6.75	3.86	n.s.
SWG	17.50	10	1.75		
Within Subj.	141.00	36			
B	33.33	1	33.33	15.62	<.01
AB	0.33	1	0.33	0.16	n.s.
B x SWG	21.33	10	2.13		
C	56.33	1	56.33	39.30	<.01
AC	1.33	1	1.33	0.93	n.s.
C x SWG	14.33	10	1.43		
BC	0.75	1	0.75	0.67	n.s.
ABC	2.08	1	2.08	1.87	n.s.
BC x SWG	11.17	10	1.12		

ANOVA 22

Mean Time of Mount (MTM) with Change of Female

Source	SS	df	MS	F	p
Total	74.98	47			
Between Subj.	12.73	11			
A	0.02	1	0.02	0.02	n.s.
SWG	12.71	10	1.27		
Within Subj.	62.25	36			
B	11.02	1	11.02	15.29	<.01
AB	3.52	1	3.52	4.88	n.s.
B x SWG	7.21	10	0.72		
C	15.19	1	15.19	16.20	<.01
AC	9.19	1	9.19	9.80	<.05
C x SWG	9.38	10	0.94		
BC	0.19	1	0.19	0.38	n.s.
AB	1.69	1	0.69	3.46	n.s.
BC x SWG	4.88	10	0.49		

ANOVA 23

Pre-Ejaculatory Thrusts (PET) with Change of Female

Source	SS	df	MS	F	p
Total	5921.98	47			
Between Subj.	1090.23	11			
A	136.68	1	136.68	1.43	n.s.
SWG	953.55	10	95.35		
Within Subj.	4831.75	36			
B	1131.02	1	1131.02	20.01	<.01
AB	165.02	1	165.02	2.92	
B x SWG	565.21	10	56.52		
C	402.52	1	402.52	4.08	n.s.
AC	15.19	1	15.19	0.15	n.s.
C x SWG	987.54	10	98.75		
BC	744.19	1	744.19	10.31	<.01
ABC	99.18	1	99.18	1.37	n.s.
BC x SWG	721.88	10	72.19		

ANOVA 24

Ejaculation Latency (EL) with Change of Female

Source	SS	df	MS	F	p
Total		47			
Between Subj.	187975936.00	11			
A	107986176.00	1	107986176.00	13.49	<.01
SWG	79989760.00	10	799897.60		
Within Subj.	247729049.60	36			
B	4633088.00	1	4633088.00	6.30	<.05
AB	2026752.00	1	2026752.00	2.76	n.s.
B x SWG	7348736.00	10	734873.56		
C	171276697.60	1	171276697.60	171.23	<.01
AC	34231296.00	1	34231296.00	34.22	<.01
C x SWG	10004480.00	10	1000448.00		
BC	7226880.00	1	7226880.00	6.70	<.05
ABC	200448.00	1	200448.00	0.19	n.s.
BC x SWG	10780672.00	10	1078067.20		

ANOVA 25

Ejaculation Duration (ED) with Change of Female

Source	SS	df	MS	F	p
Total	3171.92	47			
Between Subj.	2646.42	11			
A	258.13	1	258.13	39.66	<.01
SWG	65.09	10	6.51		
Within Subj.	525.50	36			
B	52.08	1	52.08	11.55	<.01
AB	33.33	1	33.33	7.39	<.05
B x SWG	45.09	10	4.51		
C	8.33	1	8.33	0.44	n.s.
AC	0.75	1	0.75	0.04	n.s.
C x SWG	190.42	10	19.04		
BC	85.33	1	85.33	8.04	<.05
ABC	4.08	1	4.08	0.38	n.s.
BC x SWG	106.09	10	10.61		

ANOVA 26

Post-Ejaculatory Interval (PEI)
with Change of Female

Source	SS	df	MS	F	p
Between Subj.		11			
A	13933395	1	13933395.00	5.25	<.05
SWG	26539800	10	2653980.00		
Within Subj.		12			
B	1348992	1	1348992.00	2.62	n.s.
AB	20640	1	20640.00	0.04	n.s.
B x SWG	5145136	10	514513.56		

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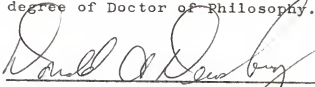   of Comparative and Physiological Psychology, 1951,
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BIOGRAPHICAL SKETCH

Dirk Walter Mosig was born in Berlin, Germany, on April 15, 1943. After living a few years in Spain, he moved to Argentina in 1948, where he attended the Colegio de la Salle (Argüello, Córdoba), graduating with the degree "Bachiller y Perito Mercantil" (with honors) in 1961. He next attended the Instituto de Matemática, Astronomía y Física of the Universidad Nacional de Córdoba for one year. In 1963 he came to the U. S., enrolling at Eastern New Mexico University, where he graduated with a Bachellor of Arts (magna cum laude) in June, 1966, majoring in Psychology. He attended the University of Florida from 1966 to 1971, majoring in Psychology and minoring in Zoology, receiving the M. A. in June 1969. He has been employed as Assistant Professor of Psychology at Georgia Southwestern College since 1971.

Among Dirk Mosig's hobbies are Karate, photography, and chess. He also has a special research interest in the life and works of the Providence, R. I. author, H. P. Lovecraft.

Dirk Mosig married Edna Alice Ramsey in 1965. They have three daughters, Laila, Aileen, and Sheila.
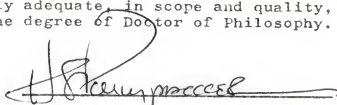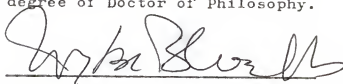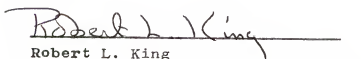
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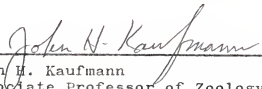
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Wilse B. Webb
Professor of Psychology

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Assistant Professor of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Department of Psychology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June, 1974

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